Abstract

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Periodical Cicada Brood Borders are Maintained by Competition and Allee Dynamics

Andrew LIEBHOLD
USDA Forest Service, 180 Canfield St., Morgantown, WV 26505, USA
Richard KARBAN
Department of Entomology, University of California, Davis, Davis, CA 95616, USA

Abstract Periodical cicadas, *Magicicada* spp., exhibit a multitude of remarkable traits. One generation requires either 13 or 17 years for completion. Most of this time is spent in nymphal stages which feed underground on tree roots. Emergence of adults at any one location is synchronized; geographically adjacent populations (referred to as a 'brood') emerge on a single year. While the geographical distribution of broods has been documented on a large scale (county-level records), little is known about their distributions at finer spatial scales. In particular, little is known about the extent to which broods overlap. We conducted a detailed survey at the adjacent margins of brood V (emerged in 1999) and brood VIII (emerged in 2002) in southwestern Pennsylvania. This survey indicated that over most of the area the broods did not overlap, though there was a small area where both broods were sympatric and a larger area where neither brood existed. We used a simulation model to explore the processes that contribute to brood boundary stability. The model combined the inverse density-dependent mortality caused by birds preying on adults and positive density dependent mortality of nymphs caused by competition. The model was parameterized using previously published field data. Simulations indicated that predation caused an Allee effect in which sparse populations always go extinct. Furthermore this Allee effect interacted with the competitive interaction in a way such that the least abundant of any sympatric broods always went extinct. This phenomenon resulted in a type of boundary 'pinning' to reinforce brood boundaries.

Induced Response of Oak Trees to *Raffaelea quercivora as* a Possible Defense against Japanese Oak Wilt Caused by the Ambrosia Fungus Carried by an Ambrosia Beetle

Kenryu KATO, Hisahito OANA, Nobuko KAKIUCHI, Masayuki MIKAGE, Naoto KAMATA
Graduate School of Natural Science and Technology, Kanazawa University, Kanazawa, Ishikawa 920-1192, JAPAN
Kojiro ESAKI
Ishikawa Forest Experiment Station, Hakusan, Ishikawa 920-2114, JAPAN
Tohru MITSUNAGA, Shin-ichiro ITO
Faculty of Bioresources, Mie University, Kamihama 1515, Tsu, Mie, 514-8507, JAPAN

Abstract Japanese oak wilt (JOW) has been recognized in Japan since the 1930s, but in the last fifteen years epidemics of this disease have intensified and spread to western coastal areas. The symbiotic ambrosia fungus *Raffaelea quercivora* is the causal agent of oak dieback, and is vectored by *Platypus quercivorus* (Murayama). This is the first example of an ambrosia beetle fungus that kills vigorous trees. Mortality of *Quercus crispula* Blume was approximately 40%. Necrosis has been observed around the gallery systems in sapwood, and has been attributed to *R. quercivora.* The necrosis stops water conductance, and a tree dies when necrosis completely blocks any cross-section of the tree. We found that many *P. quercivorus* males avoided such necrosis when they tunneled into trees that had attacked in the previous year. Gallic acid was newly produced in necrotic tissue and concentrations of ellagic acid were doubled. A laboratory experiment proved that *P. quercivorus* adults avoided the sapwood with high concentrations of gallic acid or ellagic acid. It is estimated that 0.0456% of gallic acid and 0.0260% of ellagic acid completely prevent insect tunneling. These tannic acids thus have some potential as control tools against Japanese oak wilt caused by the ambrosia fungus.

Study of *Quercus crispula* Wood Extractives Damaged from *Platypus quercivorous* Attack

Miwa KASAI, Shin-ichiro ITO, Tohru MITSUNAGA
Faculty of Bioresources, Mie University, Kamihama 1515, Tsu, Mie, 514-8507, JAPAN
Naoto KAMATA
Graduate School of Natural Science and Technology, Kanazawa University, Kanazawa, Ishikawa 920-1192, JAPAN

Abstract Discoloration of *Quercus crispula* sapwood resulting from colonization by the ambrosia beetle *Platypus quercivorus* was examined. Polyphenol analyses showed that hydrolyzable tannin was contained in healthy sapwood but diseased sapwood contained large quantities of ellagic acid and lesser amounts of gallic acid. Tannase and laccase activities were identified from *Raffaelea quercivora*, a symbiotic fungus associated with *P. quercivorus*. Purprogallincarboxylic acid bio-converted with laccase from gallic acid was contained in diseased sapwood. We conclude that the discoloration of sapwood is caused by the biological oxidation of wood extractives, especially polyphenolic compounds.

Sensory Cues for Shelter Use

Niklas BJÖRKLUND
Department of Entomology, Swedish University of Agricultural Sciences, P.O. Box 7044, SE-750 07 Uppsala, SWEDEN

Abstract Many insects spend a large proportion of their life inactive, hiding in shelters. Therefore, the presence of shelters may influence where the insects feed. I examined stimuli affecting the use of shelters by adults of the pine weevil, *Hylobius abietis* (L.), which is an economically important forest pest in Europe since the adults feed on the stem bark of newly planted conifer seedlings. When there are hiding or burrowing places present in close vicinity of a seedling, pine weevils may hide there and repeatedly return to feed on the same seedling. Experiments were conducted in a laboratory arena with above- or below-ground shelters and in the presence or absence of wind. Pine weevils were highly attracted to both above- and below-ground shelters and weevils in shelters were often observed placing themselves in a characteristic "resting" posture. Experiments with opaque and transparent shelters showed that visual stimuli are used in the orientation towards shelters and also increase the probability of remaining for a long period behind a shelter. The presence of wind increased the propensity to use both above- and below ground shelters.

Population Dynamics of Willow Leaf Beetles in Managed and Natural Willow Stands

Peter DALIN
Department of Entomology, Swedish University of Agricultural Sciences, P.O. Box 7044, SE-750 07 Uppsala, SWEDEN

Abstract It is generally believed that diversity leads to stability in ecosystems. One consequence would be that insect populations should fluctuate less in density over time in natural and diverse systems compared with managed systems. In this study, we measured densities of leaf beetles (Coleoptera: Chrysomelidae) over five years in 20 managed willow (*Salix viminalis*) plantations and in 22 natural willow (*S. cinerea*) stands. We found no significant difference in temporal variability (coefficient of variation) of leaf beetle density between managed and natural willow stands. However, outbreaks (i.e. drastic increases in leaf beetle density) tended to be more frequent in the willow plantations. In addition, leaf beetle populations showed strong negative density dependent growth in natural willow stands. No such patterns were observed in the managed willow stands. Although feedback effects were observed in the natural willow stands, this did not lead to a significantly greater stability of leaf beetle populations compared with willow plantations.

Harvesting Disrupts Biological Control of Leaf Beetles in Short-Rotation Coppice Willows

Christer BJÖRKMAN
Department of Entomology, Swedish University of Agricultural Sciences, P.O. Box 7044, SE-750 07 Uppsala, SWEDEN

Abstract Disturbances such as harvesting may interfere with the ecological processes that lead to biological control of insect pests. For willows, which are grown as short rotation coppice crops harvested every 3rd to 5th year, it has been suggested that high plant quality in the re-sprouting shoots after harvesting may explain observed high densities of herbivorous insects, especially leaf beetles (Coleoptera: Chrysomelidae), in the plantations. Here we show that generalist predators may be important as regulators of leaf beetle populations. All the three leaf beetle species, studied for five years in twelve plantations showed a negative correlation between the population growth rate from spring to fall and the abundance of the most common generalist predator *Orthotylus marginalis* (Heteroptera: Miridae). For the most abundant leaf beetle, *Phratora vulgatissima*, it was also found a significant positive correlation between its population growth rate and egg survival indicating an overall effect of predation on herbivore population growth. Harvesting, taking place during the winter had a negative effect on the abundance of leaf beetles and predators. However, the first year after harvesting, all three leaf beetle species regained this loss with a high population growth rate. A reason for the better ability of the herbivores to recover from the disturbance may be that they, unlike the predators, mainly overwinter outside the plantations. All three leaf beetle species peaked in density three years after harvesting whereas the density of generalist natural enemies increased or levelled off during the five year period after harvesting. It is concluded that predation by generalist predators is potentially important for population control of leaf beetles in willow coppice, but that the intermediate disturbance regime of around 5 years between harvests, appears to be too short to avoid disruption of biological control. Alternative harvesting regimes resulting in more efficient biological control in short rotation coppice systems may be a longer period between harvests that enables the predators to fully respond numerically, to leave natural enemies refuges at harvest, or to harvest adjacent plantations asynchronously.

Reproductive Success of the Spruce Bark Beetle *Ips typographus* and Impact of Natural Enemies in Five Years Following a Storm-Felling

Martin SCHROEDER, Åke LINDELÖW
Department of Entomology, Swedish University of Agricultural Sciences, P.O. Box 7044, SE-750 07 Uppsala, SWEDEN

Abstract After a large storm-felling in Sweden in November 1995 the reproductive success of the bark beetle *Ips typographus* and the densities of natural enemies were studied by sampling of bark from colonised trees. The study was conducted in two reserves where all storm-felled trees were left. In the first summer *I. typographus* only colonised storm-felled trees. In the second summer both storm-felled and standing living trees were colonised, while in the third to fifth summers only living trees were attacked. After the fifth summer no more trees were killed by the bark beetle. The reproductive success of *I. typographus* was highest in the storm-felled trees and decreased over the five-year period while the density of enemies increased over the same time. More than 50 % of the variation in the reproductive success of *I. typographus* could be explained by the egg gallery density of *I. typographus*. The densities of enemies did not contribute to explaining the remaining variation in reproductive success of *I. typographus*. Thus, this study indicates that intraspecific competition is an important factor contributing to terminating outbreaks of *I. typographus*.

Temporal Patterns in *Epirrita autumnata* Dynamics: Parasitoids and Other Possible Factors

Helena BYLUND, Olle TENOW
Department of Entomology, Swedish University of Agricultural Sciences, P.O. Box 7044, SE-750 07 Uppsala, Sweden

Abstract Larvae of the autumnal moth *Epirrita autumnata* (Geometridae), are defoliating different parts of the mountain birch forests in northern Fennoscandia every 9-10 years. Larval densities of *E. atumnata* were monitored during two periods, 1955-1967 and 1984-2003, at Abisko, northern Sweden. Time series analyses of density data indicated that different factors were important in the two periods. The generation rate of change in moth density was fitted in multiple regressions with the population density of the previous year and parasitism rate, as well as other factors, for each period separately and for all years together. Parasitism explained most of the variability in the second monitoring period while winter temperatures were important in the first period. First-order effects and parasitism explained 74% of the variability for all years.

Is the Parasitoid *Perilitus areolaris* a Significant Mortality Factor for Adult Pine Weevils?

Helena BYLUND, Henrik NORDENHEM and Göran NORDLANDER
Department of Entomology, Swedish University of Agricultural Sciences, P.O. Box 7044, SE-750 07 Uppsala, Sweden

Abstract *Perilitus areolaris* (Braconidae) parasitizes adult pine weevils (*Hylobius abietis*; Curculionidae). Little is known about the biology of this parasitoid and how it affects the population dynamics of the pine weevil. We collected several thousand pine weevils from spring to autumn over 3 years at 6 clear-cuttings in the southern part of Sweden. The weevils were dissected and we recorded the reproductive phase, the presence/absence of flight muscles and the presence/absence of parasitoid eggs and larvae. Preliminary analyses of the data showed that about 20% of the pre-reproductive, young weevils were parasitized at the weevil regeneration sites (1 and 2 year-old clear-cuttings). We concluded that *P. areolaris* is a significant mortality factor that decreases the production of weevils at the study sites.

Relationships between Defensive Characteristics of *Fagus crenata* Galls and the Timing of Gall Fall

Kenji TOKUNAGA, Naoto KAMATA
Graduate School of Natural Science and Technology, Kanazawa University, Kanazawa, Ishikawa 920-1192, JAPAN

Abstract Plant galls usually contain defensive chemicals, such as tannins. We measured levels of physical and chemical defenses of galls and of galled leaves of *Fagus crenata*, which were induced by six species of gall midges. Relationships between these defensive features and the timing of the fall of galls from host plants were determined. Ecological significance of defensive features of galls and galled leaves were discussed with respect to manipulation by gall inducers. We collected galled and ungalled leaves with six species of gall midges from current year shoots, in which leaves had received no damage from folivores. Dry leaf mass per area (LMA) was used as a measureof physical defense. The concentration of total phenolics and that of condensed tannins were also determined for galls and leaves. The timing of gall drop was determined from litter samples collected every month using litter traps. The LMA of galled leaves were generally greater than those of ungalled leaves. In contrast, levels of chemical defenses in galls varied greatly among gall midge species. However, levels of chemical defenses evel tended to be higher in galls that fell later in a season. These results suggest that higher levels of chemical defenses were related to longer periods of exposure to folivores.Results also appear to support the hypothesis of manipulation by gall-inducers, in which a gall-inducer manipulates the defensive traits of its gall or galled leaf to reduce the risk of mortality caused by folivores.

Linking Ecosystem Ecology to Insect Population Ecology: Nitrogen Cycling, Foliage Properties, and Insect Outbreaks

Naoto KAMATA, Yuki KUNIHISA, Lina KOYAMA
Graduate School of Natural Science and Technology, Kanazawa University, Kanazawa, Ishikawa 920-1192, JAPAN
Naoya WADA
Center for Far Eastern Studies, Toyama University, Toyama, Toyama 930-8555, JAPAN

Abstract The beech caterpillar, *Syntypistis punctatella* (Motschulsky) (Lepidoptera: Notodontidae), often causes extensive defoliation of beech forests in Japan. Outbreaks often occur synchronously among different areas at intervals of 8 – 11 years. Defoliation by this insect tends to occur at a specific range of elevations. This range of elevation varies among regions, but the outbreak zone tends to be lower at higher latitudes; e.g. 300–500 m ASL in southern Hokkaido (42°N), 600–800 m ASL in Hakkohda (40°40′N), 900–1100 m ASL in Hachimantai (40°N), and 1100–1300 m ASL in Hakusan (36°N). As a result, defoliated areas spread horizontally in altitudinal belts. Many hypotheses have been presented to explain elevation-dependent population outbreaks. In Hachimantai, five study plots were established along elevational gradients running through each plot. In each plot, beech saplings (3–5 m at height) were manually defoliated to investigate foliage quality and delayed induced response after insect defoliation. Soil nitrogen availability was determined by measuring NH_4^+ and NO_3^- concentration in soil extracts. Soil nitrogen availability and foliage quality was highest in the plot where the beech caterpillar reached outbreak levels. A positive feedback among soil nitrogen availability, foliage quality, and insect population increase were identified in the system. We hypothesized that the rate of nitrogen cycling relative to altitude is key to determining these three factors.

Semiochemical Diversity and Niche Partitioning among Scolytids and the Generalist Bark-Beetle Predator, *Thanasimus formicarius* (Coleoptera: Cleridae)

Nathalie WARZEE, Jean-Claude GREGOIRE
Lutte biologique et Ecologie spatiale, CP 160/12, Université Libre de Bruxelles, 50 avenue F.D. Roosevelt, B-1050 Brussels, BELGIUM
Hervé JACTEL, Pierre MENASSIEU
Laboratory of Forest Entomology & Biodiversity, INRA, BP45, F-33612 Cestas Cedex, FRANCE
Christian MALOSSE
Laboratory of Phytopharmacy, INRA, Route de Saint-Cyr, F-78026 Versailles Cedex, FRANCE

Abstract In southwestern France, two conspecific scolytids, *Ips sexdentatus* (Boern.) and *Orthotomicus erosus* (Woll.), share several pheromone compounds, to which their common predator, *Thanasimus formicarius* (L.), responds. This raises questions regarding the role of pheromones in niche competition between the bark beetles and in prey recognition by the predator.

In spring 2003, in a pure stand of maritime pine (25 years old) located in the Forest Research Centre of INRA (Cestas, France), four attractants of bark beetles and *T. formicarius*, (i.e.: racemic ipsdienol (I);exo-brevicomin (E); Pheroprax® the commercial pheromone of *Ips typographus*, a blend of 2-methyl-3-buten-2-ol and cis-verbenol (P); and Stenoprax® the commercial pheromone of *Ips sexdentatus*, a blend of ipsdienol and 2-methyl-3-buten-2-ol (S)), were tested in six different combinations: S, I, PI, SE, IE and PIE. Each mixture was replicated five times and the control (no attractant) was repeated twice. The 32 small "bottle-traps" (30x15 cm) were randomly set-up on a 8x4 grid and were inspected weekly from 5 May to 12 June 2003. Traps were permutated at each inspection. Differences between mean relative catches/trap/day were tested with the GLM procedure and a post-hoc Scheffe's test.

Catches of I. sexdentatus were significantly ($P < 0.001$) higher in pheromone traps loaded with S and SE blends, whereas *Orthotomicus* spp. was significantly ($P < 0.001$) more attracted by pheromone traps loaded with S, SE, PI and PIE mixtures. All the six kairomone mixtures induced higher attraction of T. formicarius than the control, although S was the only blend that induced significantly ($p < 0.001$) higher catches than the control trap.

Orthotomicus spp. responds to all the pheromone blends attractive to *Ips sexdentatus* but the reciprocal is not true. These bark beetles share the same habitat of pine forest but they have different ecological niches. The small species *Orthotomicus* lives in thin bark of pine trees and the large species *I. sexdentatus* needs thick bark to develop. For *Orthotomicus* spp., it is therefore an advantage to be able to respond to the pheromone of *I. sexdentatus* because trees attacked by the large species are likely to provide the smaller species with suitable conditions of development. The reverse is not true as the presence of *Orthotomicus* spp. does not necessarily indicate the availability of thick bark : it is then also an advantage for I. sexdentatus not to respond to the pheromone of the small scolytid species. *T. formicarius* is able to recognize and respond to any combination of the semiochemicals that compose the active pheromone of the bark beetles (*Ips* and *Orthotomicus* spp.). As a generalist predator, it is probably in its interest to respond to the pheromone of different prey, thereby enhancing the probability of finding food, a sexual partner and eventually a suitable habitat for breeding.

The results have also practical implications. Fortunately, Stenoprax® lures can be used to monitor *Ips sexdentatus*, *Orthotomicus* spp. and *Thanasimus formicarius* populations with the same pheromone traps. Unfortunately, any pheromone mass trapping of the pests (bark beetles) may adversely affect the natural enemies (*Thanasimus*).

Utilization of the Symbiotic Fungus Propagated in Host-Tree before Oviposition by a Woodwasp, *Urocerus japonicus* (Hymenoptera: Siricidae)

Hideshi FUKUDA
1Depertment of Human Environment and Information Technology, Faculty of Social and Informational Sciences, Nihon Fukushi University, Higashiehaemi-cho, Handa, Aichi 475-0012, JAPAN
Akira SANO
Mie Prefectural Science and Technology Promotion Center., Hakusan-cho, Mie 515-2602, JAPAN

Abstract Most woodwasps (Siricidae) are symbiotically associated with the specific fungus, Amylostereum spp. Female adults inoculate the fungus during their oviposition in the sapwood of host trees. Woodwasp larvae can digest sapwood with low nutritional quality with the aid of symbionts. In an earlier study, we clarified that a woodwasp with no fungal symbionts, *Xeris spectrum* can utilize the fungal symbionts of other woodwasp species without possessing any symbiotic fungi of its own. Moreover, the larvae of fungus-carrying woodwasp species cannot develop on living trees. The female adults oviposit selectively on freshly killed trees that are presumed to be suitable for fungus propagation, because the conditions of the wood at the time of oviposition affect propagation of the fungus. Whether fungus-carrying woodwasps can develop using no maternal symbiotic fungus or not has never been studied. Thus, we conducted fungus-isolation and oviposition experiments to evaluate the preference and performance of *U. japonicus* on fungus-inoculated trees.

Experiments were conducted from 1999 to 2001. In July 1999, the first year, new female adults of *U. japonicus* were allowed to oviposit on living trees of *Cryptomeria japonica* (oviposited trees). In October, the symbiotic fungus of *U. japonicus* was artificially inoculated on living trees of *C. japonica* (inoculated trees). In November, oviposited trees, inoculated trees and control (not oviposited and not inoculated) trees were felled and a portion of the inoculated trees were bucked to 2 m lengths. In July 2000, the second year, new female adults were allowed to oviposit on each tree. At the same time, fungi were isolated from both oviposited and inoculated trees. In 2001, the third year, we counted the number of new adults that emerged from each tree where oviposition occurred in the 2nd year, and we also counted oviposition holes on each tree.

The inoculated symbiotic fungus propagated on both oviposited trees and inoculated trees 8 months after tree-felling, during the oviposition period of the next year. Moreover, the symbiotic fungus was distributed widely in the wood of inoculated trees, especially on bucked trees. Oviposition by *U. japonicus* was higher on oviposited and inoculated trees than on control trees; moreover, oviposition was higher on inoculated than on oviposited trees. On inoculated trees, many oviposition holes were observed near vertical lines from inoculated positions, where the symbiotic fungus had propagated vigorously. Next generation adults emerged from inoculated trees, whereas no adults emerged from oviposited and control trees. The number of emerged adults was especially high on bucked trees. From these results, we demonstrated that a fungus-carrying woodwasp species, *U. japonicus*, can reproduce using no maternal symbiotic fungus. Combined with results from a previous study, these results indicate that both *X. spectrum*, a woodwasp species that has no maternal symbiont, and *U. japonicus* a fungus-carrying woodwasp species, can utilize the *Amylostereum* fungi which had already propagated in the wood. This information is important for clarifying the coevolution between woodwasps and *Amylostereum* fungi.

KEY WORDS: *Amylostereum* fungus, fungus-isolation, oviposition preference, survival rate, *Urocerus japonicus*

Reaction of the Ambrosia Beetle *Platypus quercivorus* to Gallic Acid and Ellagic Acid in Oak Sapwood

Hisahito OANA, Nobuko KAKIUCHI, Masayuki MIKAGE, Naoto KAMATA
Graduate School of Natural Science and Technology, Kanazawa University, Kanazawa, Ishikawa 920-1192, JAPAN
Kojiro ESAKI
Ishikawa Forest Experiment Station, Hakusan, Ishikawa 920-2114, JAPAN
Tohru MITSUNAGA, Shin-ichiro ITO
Faculty of Bioresources, Mie University, Kamihama 1515, Tsu, Mie, 514-8507, JAPAN

Abstract The ambrosia beetle, *Platypus quercivorus* (Coleoptera: Platypoididae) (Maruyama), is a critical vector of the fungus, *Raffaelea quercivora*. Inoculation of *R. quercivora*, causes necrosis in sapwood, stops water conductance, and kills host trees. *Platypus quercivorus* constructs galleries in oak sapwood, avoiding necrosis formed by attacks of the same species in the previous year. Reproductive success of *P. quercivorus* was greatly decreased on host trees that were attacked in the previous year because there was less space for galleries in the second year. In most cases, *P. quercivorus* could not reproduce at all on trees with a previous infestation history. If *P. quercivorus* avoid necrosis in response to chemical substances, then these chemicals may be useful tools for preventing *P. quercivorus* attacks. Gallic acid is not detected from healthy sapwood but is detected (0.001% wet weight) in necrotic tissue. Concentration of ellagic acid is higher (0.050% wet weight) in necrotic tissue than in healthy sapwood. To test the effect of gallic acid and/or ellagic acid on behavior of gallery construction by *P. quercivorus*, male beetles were introduced to oak xylem in which gallic acid and/or ellagic acid concentrations were experimentally elevated. Results indicated that *P. quercivorus* avoided high concentrations of gallic acid and ellagic acid. These results coincided with previous reports obtained by field observations and by inoculation experiments indicating that *P. quercivorus* avoiding necrosis when constructing galleries. Gallic acid did not disturb gallery construction of *P. quercivorus* at the same low concentration found in necrosis. In contrast, ellagic was capable of terminating gallery construction completely. These results suggest that ellagic acid plays a critical role in the avoidance of necrosis during *P. quercivorus* gallery construction.

Volatile Compounds Related to Attractant of *Platypus quercivorus* (Murayama) from *Quercus crispula*

Hiroyuki TAKEMOTO, Shin-ichiro ITO, Tohru MITSUNAGA
Faculty of Bioresources, Mie University, Kamihama 1515, Tsu, Mie, 514-8507, JAPAN
Naoto KAMATA
Graduate School of Natural Science and Technology, Kanazawa University, Kanazawa, Ishikawa 920-1192, JAPAN
Masahide KOBAYASHI
Kyoto Prefectural Forestry Experimental Station, Honjo, Tanba, Funai,Kyoto 621-1121, JAPAN

Abstract The mass mortality of oak trees in Japan is expanding due to the vector, *Platypus quercivorus* (Murayama), which bores into the trunks of oaks and other angiosperm trees. We analyzed the volatile compounds emitted from the tissues of the most frequently attacked host tree, *Quercus crispula*. We also investigated relationships between several compounds identified and the attractive responses of the beetle. Results from the bioassays showed that toluene, 3-octanone, anisole and 1-hexadecanal are probably attractant compounds for *P. quercivorus*.

Stand-Level Distribution and Movement of *Platypus quercivorus* Adults and Spatial Patterns of Attacks

Kojiro ESAKI
Ishikawa Forest Experiment Station, Hakusan, Ishikawa 920-2114, JAPAN
Kenryu KATO, Naoto KAMATA
Graduate School of Natural Science and Technology, Kanazawa University, Kanazawa, Ishikawa 920-1192, JAPAN

Abstract Flying populations of an ambrosia beetle, *Platypus quercivorus* (Murayama), a vector of the ambrosia fungus *Raffaelea quercivora*, which causes Japanese oak wilt in Japan, were sampled using sticky screen traps. *Platypus quercivorus* beetles tend to move upwards along slopes. The highest concentrations of flying beetles usually occur at the upper forest margins. During the period when numbers of flying beetles were increasing, the incidence of newly infested trees spread from the epicenter into the forest. During the period when number of flying beetles is decreased, the epicenter shrank into the upper forest edge. Newly infested trees did not occur in this period because most trees had already been infested. Near the upper forest edge, where many beetles were highly concentrated throughout the season, the number of new entry holes decreased considerably after the initial attack, early in the season, though many adults were present throughout the entire period.

Influence of Light Condition on the Spatial Distribution of an Ambrosia Beetle *Platypus quercivorus* (Murayama) (Coleoptera: Platypodidae) Flying in a Natural Secondary Broad-Leafed Forest

Yutaka IGETA, Kenryu KATO, Naoto KAMATA
Graduate School of Natural Science and Technology, Kanazawa University, Kanazawa, Ishikawa 920-1192, JAPAN
Kojiro ESAKI
Ishikawa Forest Experiment Station, Hakusan, Ishikawa 920-2114, JAPAN

Abstract *Platypus quercivorus* (MURAYAMA) is known to be the primary vector of *Raffaelea quercivora* that causes oak mortality in Japan. Differing from many Scolytid and Platypodid species, *P. quercivorus* attacks healthy host trees and sometimes kills them. In this study we examined adult phototaxis in a laboratory experiment, we investigated the spatial distribution of adults flying in and around forest gaps and we investigated light conditions relative to the distribution of adults in the field. Results of the phototaxis experiments indicate that newly emerged adults of *P. quercivorus* are positively phototactic. The distribution of *P. quercivorus* at the stand level was influenced by light conditions. The behavioral response of *P. quercivorus* to light may therefore explain their tendency to invade trees around roads and forest gaps.

Analysis of Japanese Oak Wilt Spread Using Aerial Photography and GIS

Ryotaro KOMURA, Naoto KAMATA, Ken-ichiro MURAMOTO
Graduate School of Natural Science and Technology, Kanazawa University, Kakuma, Kanazawa, Ishikawa 920-1192, JAPAN
Andrew LIEBHOLD
Northeastern Research Station, USDA Forest Service, 180 Canfield St, Morgantown, WV 26505 USA
Koujiro ESAKI
Ishikawa Forest Experiment Station, Hakusan, Ishikawa 920-2114, JAPAN

Abstract In Japan, Japanese oak wilt (JOW) has been known since the 1930s. In the decades directly following its initial discovery, JOW epidepmics were only a few years in duration and were confined to only a few areas on the Japan Sea (western) coast of Japan. However, in the last ten years epidemics have intensified and spread to the island's western coastal areas. The symbiotic ambrosia fungus *Raffaelea quercivora* is the causal agent of oak dieback, and is vectored by *Platypus quercivorus* (Murayama). This is the first example of an ambrosia beetle fungus that kills vigorous trees. We provide here an analysis of the historical distribution and spread of JOW previously recorded at the regional scale . Additionally of mortality caused by JOW at the stand scale level was investigated using aerial photographs. In this study, statistical analysis of spread of the oak diebacks was done conducted using a geographical information system (GIS) and rates of JOW spread were among different spatial scales. Results suggest that spread is the result of long, middle and short distance movement by adult beetles.